Evaluating the effectiveness of restoring longitudinal connectivity for stream fish communities: towards a more holistic approach

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Abstract

A more holistic approach towards testing longitudinal connectivity restoration is needed in order to establish that intended ecological functions are achieved. We illustrate the use of a multi-method scheme to evaluate the effectiveness of 'nature-like' connectivity restoration for stream fish communities in the River Deerness, NE England. Electric-fishing, capture-mark-recapture, PIT telemetry and radio-telemetry were used to measure fish community composition, dispersal, fishway efficiency and upstream migration respectively. For measuring passage and dispersal, our rationale was to evaluate a wide size range of strong swimmers (exemplified by brown trout *Salmo trutta*) and weak swimmers (exemplified by bullhead *Cottus perifretum*) *in situ* in the stream ecosystem. Radio-tracking of adult trout during the spawning migration showed that passage efficiency at each of five connectivity-restored sites was 81.3-100%. Unaltered (experimental control) structures on the migration route had a bottle-neck effect on upstream migration, especially during low flows. However, even during low flows, displaced PIT tagged juvenile trout (total n = 153) exhibited a passage efficiency of 70.1-93.1% at two nature-like passes. In mark-recapture experiments juvenile brown trout and bullhead tagged (total n = 5303) succeeded in dispersing upstream more often at most structures following obstacle modification, but not at the two control sites, based on a Laplace kernel modelling approach of observed dispersal distance and barrier traverses. Short-term post-restoration data (2-3 years) showed that the fish assemblage remained similar at five of six connectivity-restored sites and two control sites, but at one connectivity-restored headwater site previously inhabited by trout only, three native non-salmonid species colonised. We conclude that stream habitat reconnection should support free movement of a wide range of species and life stages, wherever retention of such obstacles is not needed to manage non-native invasive species. Evaluation of the effectiveness of fish community restoration in degraded streams benefits from a similarly holistic approach.

Keywords: habitat fragmentation, fish assemblages, passage efficiency, telemetry, PIT, VIE

1. Introduction

Due to resource exploitation by humans, river habitats have become increasingly fragmented (Poff *et al.* 1997; Nilsson *et al.* 2005), threatening aquatic species' abundance, distribution and diversity (e.g. Dunham *et al.*1997; Vaughn and Taylor 1999; Khan and Colbo 2008) and wider ecosystem integrity (Fahrig 2003; Pringle 2003). Loss of connectivity between river habitats is often a result of construction of physical obstacles to migration and dispersal, such as dams, weirs and culverts (e.g. Morita and Yamamoto 2001; Gehrke *et al.* 2002; Park *et al.* 2008; Doehring *et al.* 2011; Hall *et al.* 2011). Much attention has been paid to the partial or complete blocking effects of obstructions on the migration success and population persistence of diadromous fishes, migrating between freshwater and marine environments (McDowall 1992; Baras and Lucas 2001). Obstacles may also be strongly detrimental to species migrating or dispersing entirely in freshwater (Lucas and Batley 1996; Porto *et al.* 1999; Branco *et al.* 2012; Gough *et al.* 2012; Benitez *et al*. 2015). Dispersal is crucial for population persistence and is intrinsic to ecological, behavioural and evolutionary processes (McMahon and Matter 2006; Urban *et al.* 2009). Longitudinal reconnection is increasingly a major goal of river restoration (Fullerton *et al.* 2010; Kemp and O'Hanley 2010).

Rehabilitation of stream ecosystem function and biodiversity often requires reversal of the impacts of multiple stressors (Palmer *et al.* 2005; Bernhardt and Palmer 2007; Fullerton *et al.* 2010; Wohl *et al.* 2015). For example, improvements in water quality and physical habitat diversity, and reinstatement of more natural hydraulic connectivity may be needed to support a more abundant and diverse fish assemblage (Van Dijk *et al.* 1995; Bernhardt and Palmer 2007). Degraded aquatic communities can recover from past environmental insults only if recolonization opportunities are provided (Langford *et al.* 2009). Where past pollution incidents, for example, have eliminated populations in river reaches, recolonization requires dispersal from adjacent population sources. Downstream fish dispersal is usually relatively easy, including by passive means, but under certain conditions, for example in reservoirs located upstream of hydroelectric dams, downstream-dispersing fish may encounter migration delay, injury or even mortality when traversing the structure (Lucas and Baras 2001). In depopulated low-stream-order channels, recolonization is much more likely to entail upstream movement. Strongly-swimming species such as adult salmonids may pass small obstacles in order to access such habitat for spawning and resultant nursery habitat (Ovidio and Philippart 2002), while in other cases deliberate restocking has been used to aid recolonization (Cowx 1994). However, most species in fish assemblages are not of economic importance and many are small, with a limited ability to pass upstream of physical obstacles (Utzinger *et al.* 1998; Warren and Pardew 1998; Helfrich *et al.* 1999; Bolland *et al.* 2009). Nevertheless, they can contribute markedly to diversity and ecosystem function. If stream and river rehabilitation practices are to be effective in restoring diverse habitats and natural communities then they need to facilitate bidirectional dispersal of native fishes and other animals, not just enable concerted migrations of a few economically important species (Calles and Greenberg 2007, 2009; Gough *et al*. 2012). Such an approach is needed to address the hydromorphological modifications that, in many cases, are inhibiting restoration towards the reference assemblage conditions ('good ecological status') required by the European Water Framework Directive (WFD) (Kemp and O'Hanley 2010).

The preferred method of reinstituting effective longitudinal connectivity is physical removal of obstructions where possible (Poff and Hart 2002; Garcia de Leaniz 2008). Obstruction removal is sometimes not feasible due to budgetary constraints, flood risks or cultural history reasons. To improve migration and dispersal connectivity, passes for various biota (mostly fish) have been developed and evaluated (Clay 1995; Larinier and Travade 2002; Roscoe and Hinch 2010; Bunt *et al.* 2012; Noonan *et al.* 2012). However, an adequate understanding of the ecological response to barrier removal or mitigation (provision of passes for biota) is required in order to prioritize restoration efforts and maximize returns on an often limited budget.

To be valuable in river restoration, fish passes should operate effectively for a wide range of species yet often they are of limited efficacy for target species (e.g. salmonids) (Aarestrup *et al.* 2003; Caudill *et al.* 2007) or the wider fish community (Mallen-Cooper and Brand 2007; Bunt *et al.* 2012; Foulds and Lucas 2013). In recent decades more effort has been made to improve longitudinal connectivity for a greater proportion of native fish species, including by barrier removal, use of low-gradient technical passes and nature-like passage solutions (Jungwirth 1996; Calles and Greenberg 2007; Gough *et al.* 2012). The effectiveness of particular fishway designs for fish taxa has been compared in several reviews (Roscoe and Hinch 2010; Bunt *et al.* 2012; Noonan *et al.* 2012).

Increased emphasis has also been placed upon predicting the most effective methods of reducing fragmentation at a catchment scale (Kemp and O'Hanley 2010; Bourne *et al*. 2011). However, few empirical studies have examined the effects of connectivity restoration both at individual sites and on a wider spatial scale for fish communities. Ideally such studies should employ methods to describe changes in community composition and species abundance, combined with those measuring colonisation and migration processes (Lucas and Baras 2001). Where possible they should also incorporate a before-after-treatment-control (BACI) design (Pretty *et al.* 2003). The most commonly available data by which river managers can attempt to evaluate the outcomes of stream connectivity restoration on fishes are quantitative or semi-quantitative fish surveys, including those required for the European WFD (Jepsen and Pont 2007). However, the degree to which fish community data, combined with environmental and GIS analyses can reflect connectivity processes in rivers with barrier networks (Branco *et al*. 2012) is debatable.

This study aimed to measure the effectiveness of reconnection of a tributary stream on the fish assemblage structure and in terms of movements of key species and life stages. A combination of quantitative community sampling, capture-mark-recapture and telemetry methods were employed in a BACI approach, within the constraints of limited control over the timing of restorative activities at different sites. The utility of this multi-method, more holistic, approach to better understand how stream fishes with strong or weak dispersal potential respond to barrier removal is discussed.

2. Methods

2.1. Study site

The River Deerness (source: lat. 54.747910, long. -1.8004704; 275 m above sea level), NE England, flows eastwards for 14.6 rkm through mixed agricultural land and woodland cover, with the riparian zone mostly consisting of semi-natural woodland and shrubs, before it joins the River Browney, a tributary of the lower River Wear. The Deerness (mean annual discharge in lower reaches *ca.* 0.5 $m^3 s^{-1}$) and Browney respond rapidly to rainfall and the subcatchments are characterised mostly by pool-riffle-run habitats, dominated by cobble and gravel substrate. Annual maximum and minimum temperature in the Deerness, calculated from 15 min interval measurements, was lowest in December (mean: 4.6 °C, mean [range] of lower 5%: 2.6 °C [2.6 - 2.8 °C] and highest in July (mean: 15.4 °C, upper 5%: 18.1 °C [17.6 - 19.0 °C]. Several villages are close by and there is extensive public access to riparian areas. The subcatchments have a coal mining heritage and have been impacted by industrial pollution, mostly associated with coal mining and coking activities from the middle of the 19th century to the late 1960s, which caused poor water quality throughout much of the Deerness (Emery 1984). In the early 1970s, substantive remediation actions commenced to counter the habitat degradation and pollution. Since then, Deerness water quality has dramatically improved although phosphorus levels still exceed targets (Environment Agency, England, 2016), largely due to diffuse inputs. By 1973, indicators of biological water quality were shown to have improved in the main Wear and in the Deerness through, for example, high abundance of Baetidae and Ephemerellidae (Brown 1974), macro-invertebrate mayfly families indicating moderate to high water quality.

Currently, the Deerness fish fauna consists mainly of the sea-going and freshwater-resident morphotypes of brown trout (*Salmo trutta*), together with bullhead (*Cottus perifretum*, part of the European *Cottus* species complex), European minnow (*Phoxinus phoxinus*) and stone loach (*Barbatula barbatula*). European eel (*Anguilla anguilla*) and grayling (*Thymallus thymallus*) are very sparsely distributed throughout the Deerness. It is 'trout-minnow zone' in the Huet fish zonation scheme. Atlantic salmon (*Salmo salar*), although now again abundant in the Wear, due to water quality improvements since the 1960s, is currently absent in the Deerness and rare in the Browney (P. Frear, Environment Agency, *pers. comm*.). No fish stocking occurs in the Deerness. River engineering development along the Deerness over the last two centuries has resulted in numerous channel modifications, some of which degraded or were lost, and others which were built or updated throughout the 20th century, particularly at numerous road crossings. In 2012-13 eight in-channel engineered structures were identified on the Deerness and its tributaries (***Fig. 1***) likely hindering fish movement, comprising, from downstream to upstream, a stepped weir and bridge support (hereafter termed site 1 (S1)), a vertical weir and a pipe-bridge crossing ford (S2 and S3, respectively), four pipe bridge fords (S4, S5, S6, S7), and a pipe culvert (S8) (***Supp. Fig. 1***). Of these eight structures, connectivity was improved at six during the study, allowing for before and after conditions to be used in analyses, while two were retained as unaltered control sites (***Table 1***).

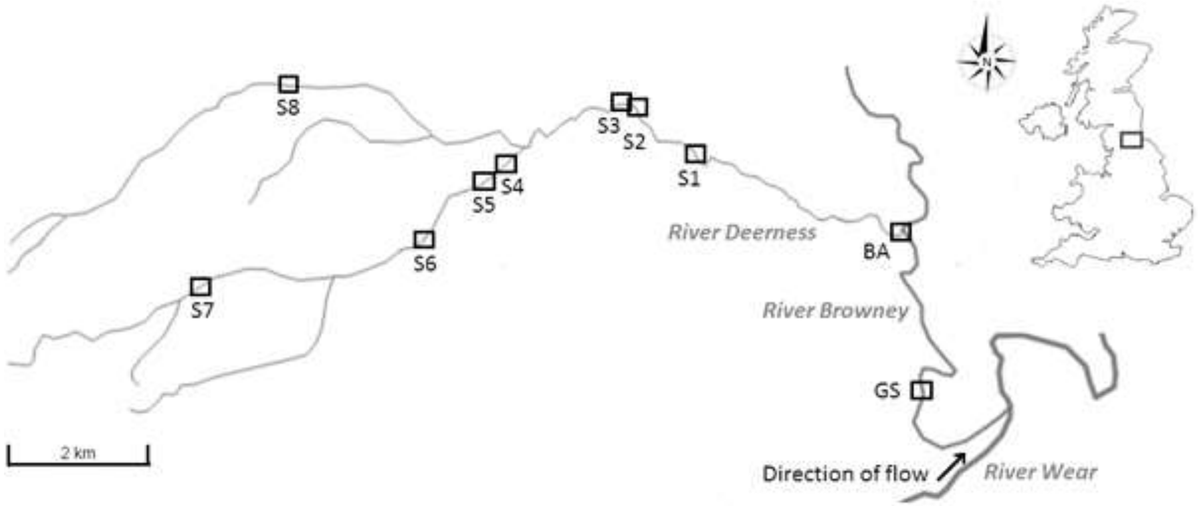

Figure 1**:** Study area within the River Wear catchment and, inset, within Britain. In addition to the eight structures on the Deerness sampled in this study (S1-S8), a further two are located on the lower Deerness (a bridge apron, BA, modified in March 2015) and lower Browney (a flow-gauging station, GS, unrestored for fish passage up to end of study).

Table 1: Details of eight in-stream structures on the Deerness, ordered from downstream (ds) to upstream (us). Vertical step (100% gradient) was measured at low summer baseflow (~Q_{98}). Note that the vertical step may be drowned out at all structures except for S1 and S2 (*) when water levels are elevated. Mpbc: multi-pipe-bridge crossing. Mean flow velocities over the structure pre-restoration and over/through structure/modification post-restoration (e.g. for S1 through rock ramp, for S2 through bypass channel) were measured at low summer baseflow, except for S8 pre-restoration (**, ~Q_{70}). ***: At the pipe culvert the nature-like pool-weir pass removed the vertical step at the perched outlet and drowned the lower part of the culvert.

Site	Structure (before)	Structure (after) (finished in)	Length (m)	Width (m)	Vertical step	Head (m)	Mean gradient	Mean (range) flow velocity pre- ; post-restoration (m s^{-1})	Notes (pre: structure pre-restoration, post: designed structure for reconnectivity during study)
S1	Stepped weir	Part-width rock ramp	13.98	15.4	1.35*	1.60	11.4	0.22 (0.12 - 0.40); 0.27 (0.06 - 0.61)	Pre: five steps, 0.05, 0.30, 0.33, 0.29 and 0.35 m (ds-us) Post: 17.08 m long, 4 m wide, 8.3 % mean gradient
S2	Weir	Nature-like bypass (Oct ’13)	1.95	13.2	0.68*	1.39	71.3	0.11 (0.03 - 0.41); 0.24 (0.08 - 0.37)	Pre: step preceded by 2.07 m long, 24.9 % gradient slope Post: 36 m long, 2 m wide, 2.7 % gradient channel with 10
S3	Mpbc	No action (control)	4.36	7.2	0.08	0.17	3.9	0.33 (0.14 - 0.40)	Pre: Bridge with 11 smooth pipe culverts, ø : 0.54 m Post: *n.a.*
S4	Mpbc	Single span bridge (April ’14)	3.76	7.8	0.10	0.12	3.2	0.26 (0.18 - 0.29); 0.11 (0.06 - 0.13)	Pre: Bridge with 7 smooth pipe culverts, ø : 0.90 m Post: Bridge replaced crossing
S5	Mpbc	Single span bridge (April ’14)	3.85	7.8	0.13	0.15	3.9	0.24 (0.12 - 0.34); 0.14 (0.09 - 0.16)	Pre: Bridge with 7 smooth pipe culverts, ø : 0.90 m Post: Bridge replaced crossing
S6	Mpbc	Single span bridge (August ’14)	3.4	4.1	0.11	0.14	4.1	0.21 (0.10 - 0.27); 0.18 (0.10 - 0.30)	Pre: Bridge with 4 smooth pipe culverts, ø : 0.60 m Post: Bridge replaced crossing
S7	Mpbc	No action (control)	11	5.4	0.29	0.34	3.1	0.22 (0.14 – 0.29)	Pre: Bridge with 2 smooth pipe culverts, ø : 0.80 m Post: *n.a.*
S8	Pipe culvert	Nature-like pool-weir (Oct ’12)***	30.3	4.5	0.26	0.65	2.1	0.37 (0.19 - 0.72)**; 0.16 (0.09 - 0.29)	Pre: Single corrugated pipe culvert, ø : 2.30 m Post: pool-weir at mouth, 4 pools, 2 - 3.3 m long

2.2. Study design

The restoration rationale was to remove anthropogenic obstructions where possible and where not, to use nature-like passage approaches, so as to facilitate natural river processes and support dispersal of aquatic biota (Jungwirth 1996; Garcia de Leaniz 2008). Obstructions located at S4, S5 and S6 were removed by conversion to single span, full-channel width bridges with natural substrate. Connectivity mitigation measures were implemented at S1 (rock ramp), S2 (nature-like bypass) and S8 (nature like pool-weir pass to culvert entrance), while S3 and S7 were left unrestored during the study and provided site controls over the study duration. Most structures were removed/modified between October 2013 and April 2014, with the exception of S8 (October 2012), S6 (August 2014) and BA (March 2015).

Several methods were used during the study period (September 2012 - July 2015) to evaluate the impacts of aforementioned in-stream structures and their removal or mitigation on passage efficiency, dispersal, and fish assemblage structure. Movement studies examined a strong swimmer, brown trout, and a weak swimmer, bullhead (Cottidae, typical of a benthic swimming guild) to reflect the breadth of swimming performance. Bullhead is an EU Habitats Directive listed species, typical of swiftly-flowing streams but lost from many watercourses for which even small obstructions restrict its distribution and recolonization potential (Utzinger *et al.* 1998; Knaepkens *et al.* 2006). Experimental work, including tagging, was authorised by ethical review committee and done under UK Home Office Licence (PPL 40/3425), in accordance with the Animals (Scientific Procedures) Act 1986. All fish surveying was authorised by the Environment Agency.

2.3. Habitat, environmental conditions and macroinvertebrates

Two vertically mounted sensors (Onset HOBO U20 Water Level Data Logger, U20-001-01) logging water temperature and pressure were deployed, one 120 m downstream of S2 and another one 100 m downstream of S8, operational from July 2013 to July 2015. Water temperature and water level were recorded every 15 minutes (± 0.44 °C and ± 0.33 kPa (0.5 cm water level), respectively). Mean daily discharge data at GS were obtained from the Environment Agency. River habitat surveys (SFCC

2007) were conducted immediately downstream (80 m long) and upstream (80 m long) of each Deerness structure (n = 8).

Insight into biological water quality (by contrast to restoration of physical connectivity) and the diversity of food resources for invertebrate-feeding fishes was gained from benthic macroinvertebrate assemblages, sampled biannually (May, October) upstream of six structures (S1, S2, S4, S6, S7, S8) from autumn 2012 to autumn 2014. It is assumed that because of limited distance between S2 and S3 (0.12 rkm) and between S4 and S5 (0.14 rkm), one invertebrate sample at each location adequately represented the biotic index for the river section in which the two structures are situated. In each sample, all in-stream habitats were kick sampled in proportion to their occurrence, for a total of 3 minutes plus one minute manual search. Invertebrates were identified to family level. A MINTA score, a biotic index of river habitat water quality, was derived by using ASPT (average score per taxon), N-TAXA (number of taxa) and BMWP (Biological Monitoring Working Party) score data (Davy-Bowker *et al.* 2008), together with relevant predictor environmental and habitat data as input for the software package River Invertebrate Classification Tool (SEPA 2016).

2.4. Fish assemblages and densities

To determine fish assemblages and the density of species above and below each of the Deerness structures, quantitative depletion electric fishing (Electracatch, WFC4, 2.5A maximum output, 50/100 Hz) was performed in July 2013-2015 at S1-S8 and in September 2012 at S7 and S8 only. Using stop nets (4 mm mesh), fish were sampled within two 80 m reaches, one immediately upstream and one immediately downstream of each (reconnected) obstacle, each incorporating multiple flow types (principally riffle, glide, pool) to increase the likelihood of representing all species within the local fish assemblage. Three passes of fishing were performed on each occasion, obtaining progressive depletion, and fish densities calculated according to Carle and Strub (1978). Fish removed in each run were temporarily kept in separate, aerated tubs. Once all runs were finished, species and body length were recorded for all fish per pass through and the fish were released back to the sample site. At sites S7 and S8, furthest upstream, where in 2012 only brown trout were caught, survey lengths were extended (single pass fishing, up to *ca.* 700 m above the structures) to confirm the absence of other species in 2012 and to record the extent of colonisation in subsequent years.

2.5. Capture-mark-recapture surveys of dispersal and passage

In order to measure natural dispersal of juvenile brown trout (strong swimmer) and bullhead (weak swimmer) and record upstream and downstream passage past river structures, capture-mark-recapture (CMR) employing electric fishing in adjacent 20 m zones, enclosed with stop nets, was used at S1-S8. Zones centred on the site of an obstacle, or former obstacle, and progressed away from it, upstream and downstream of the obstacle / former obstacle location. This was done before and after (in summer-autumn 2013 and 2014) modifications to most structures (treatment sites), or at unaltered structures (control sites). On each fishing date, one electric fishing pass-through was carried out in each zone and all fish caught were kept in zone-specific aerated tubs. Trout and bullhead over 50 mm long were tagged under anaesthesia (Bolland *et al.* 2009) with passive integrated transponder (PIT) tags or visible implant elastomer (VIE), dependent on body length. VIE tagging was site, zone- and date-specific and multiple colours and tag locations were selected for injecting the elastomer beneath the epidermis, so that it remained externally visible (***Supp. Fig. 2***). Fish of 50-79 mm were VIE tagged, while those ≥ 80 mm but ≤ 90 mm were tagged in the body cavity with an 8 x 1.4 mm PIT tag (0.027 g in air) using a needle injector. For individuals > 90 mm but < 120 mm, a 12 x 2.12 mm PIT tag (0.1 g in air) was used, while fish ≥ 120 mm were tagged with a 23 x 3.65 mm PIT tag (0.6 g in air). All trout < 90 mm were categorised as age 0+ (in the first year of life) fry, while over 95% of trout > 90 mm were age 1+ or 2+ parr based upon length-frequency distribution analysis (FiSAT tool, FAO 2016). For 12 and 23 mm PITs, a mid-ventral scalpel incision was made and the tag inserted into the body cavity. Following recovery (*ca.* 15 mins), fish were released in the centre of their 20 m capture zone.

Recapture surveys were performed as single passes in the same 20 m zones. The number of zones fished increased upstream and downstream for successive recapture surveys. Distance fished was up to 240 m above and below the structure at the last recapture survey each year, following a method of 3, 7, 10, 12 zones surveyed each side of the structure on successive survey dates. This allowed for fish movement between survey zones including possible passage over the structure (upstream or downstream), and between sites, to be studied. Three recapture surveys, following the initial tagging survey, were performed with ~3 week intervals from July to October in 2013 and 2014 at S1-S8. On resurvey, sampled fish were carefully checked for tags, and a VIE or PIT tag applied to unmarked fish. Recaptured individuals were released into the zone in which they were caught on that occasion (not necessarily the original release zone). If a recaptured fish was VIE tagged already, it was VIE tagged again with a new zone- and date-specific mark combination to allow for an assessment of movement between zones on multiple occasions (***Supp. Fig.2***). If recaptured fish had grown sufficiently, they were PIT tagged instead of being given a new VIE mark. Over the two tagging periods (summer 2013 and 2014), a total of 5303 trout and bullhead were tagged.

2.6. Upstream passage efficacy of homing juvenile trout

In order to evaluate permeability of several in-channel structures before modification, 12-25 cm trout were caught 10-200 m upstream of the structures by electric fishing, PIT tagged and displaced 20-50 m downstream of the structure in August 2012, thereby stimulating their homing behaviour (Armstrong and Herbert 1997). In September 2012, after 2-3 weeks at liberty, including during elevated flows (~Q_5-Q_{80} annual flow exceedance), recapture surveys of treatment groups (displaced from above to below structure) and control groups (displaced a short distance downstream (*ca*. 150 m), but not over the structure) were used to assess the permeability of S1, S2, S3 and S8, before restoration.

Upstream movement of displaced PIT tagged juvenile trout was used to evaluate passage efficiency during low water conditions. These displacements, in which trout were captured 20-200 m upstream of the structure and released ~30 m downstream of the pass, were performed at S2 and S8 in autumn 2014. Passage attempts and success rates were recorded with half-duplex PIT logging systems (Bolland *et al.* 2009), with interrogating antennas placed at the downstream entrance and upstream exit of the fishway. The system was operational > 99.9% of the time during each 5-6 day study and was tested daily for detection efficiency with a pole-mounted 23 mm PIT tag, comprising 50 passes (slow, ~ 0.1 m/s and fast, ~ 1 m/s) through the downstream and upstream antennas. Tag detection efficiencies (mean ± SD) were 97.3 ± 3.3 % and 96.7 ± 3.0 % respectively at downstream and upstream antennae for S2; 96.7 ± 3.0 % and 97.3 ± 2.1 % for S8 (Sep 2014); 94.7 ± 4.1 % and 93.3 ± 3.3 % for S8 (Nov 2014).

2.7. Radio telemetry of trout during the spawning migration

Passage efficiency at engineered structures, was evaluated for adult trout during the 2014 spawning migration by radio telemetry, including tagging of adult trout prior to their entry into the Deerness. Penetration through the Deerness spawning tributary could potentially be hindered by the eight structures mentioned earlier (two of which were unrestored) and two further (unrestored) structures; a bridge apron (BA) situated 20 m upstream of the Deerness/Browney confluence (DBC, ***Fig. 1***), with a 0.15 m vertical drop at the downstream end and shallow (< 5 cm) water depth across the apron width during base flow (restored in March 2015), and, on the lower Browney, a Crump-weir flow-gauging station (GS, ***Fig. 1***) without a fish pass but with a pre-impoundment to raise tailwater levels (combined head, 1.9 m at Q_{50} discharge). Consequently, all structures identified on the Deerness as well as the additional structures on the Deerness and Browney (BA and GS) were included in the radio tracking sessions.

Sea trout (n = 32) on their upstream spawning migration, and river-resident brown trout (n = 7) were caught on the lower Deerness and lower Browney by electric fishing over five sessions (22 Oct 2014 - 13 Nov 2014 (***Table 2***)). Trout were tagged under anaesthesia with a 173 MHz transmitter (ATS model F1040 / F1440) in combination with a 23 or 32 mm x PIT tag and released upon recovery (***Table 2)*** based on the methods of Bolland *et al.* (2008). Manual tracking, following the methods of Bolland *et al.* (2008), was conducted six days per week, from 22 Oct 2014 through 23 Dec 2014, and 12-21 Jan 2015 (63 tracking days). Tracking extended over a combined length of *ca*. 33 km of Browney-Deerness channel to 500 m upstream of S7 and S8. Cross-channel paired antenna PIT stations set up for a related study (Winter *et al.* 2016) at three locations on the lower Deerness (0.81 rkm, 2.31 rkm and 5.37 rkm upstream of DBC) provided temporal and direction detection data.

Table 2: Adult brown trout (river-resident) and sea trout tagging dates and release locations (ds: downstream, us: upstream) for tracking during the spawning migration. B: released in lower Browney, D: released in lower Deerness. Mean fork length (cm) and range in parentheses.

Date	Release location	Brown trout PIT + radio-tagged	Sea trout PIT + radio-tagged
22 Oct 2014	550 m ds GS (B)	1 (35.5)	4 (54.8; 40.7 - 75.4)
23 Oct 2014	400 m ds GS (B)	1 (35.0)	9 (55.0; 44.9 - 72.0)
29 Oct 2014	480 m ds GS (B)	0	11 (56.9; 45.5 - 68.0)
12 Nov 2014	350 m ds S1 (D)	5 (26.8; 22.7 - 33.5)	1 (52.6)
13 Nov 2014	40 m us BA (D)	0	7 (53.6; 49.2 - 60.5)

2.8. Statistical analyses

Analyses (Kruskal-Wallis tests; Mann-Whitney U tests; Wilcoxon signed rank tests) were performed using SPSS version 22, with an α level of significance of 0.05. Length comparisons between groups of fish which succeeded or failed to pass barriers, combined for all sites, were performed using parametric, normally distributed data, while other tests used were non-parametric. For the displacement study of juvenile trout, time taken for trout to locate the fishway, duration of ascent and length distributions among the three displacement studies were tested using Kruskal-Wallis and Mann-Whitney tests. Wilcoxon signed rank tests were performed to test for significant differences in body length of brown trout that traversed a structure in an upstream or downstream direction relative to body length of individuals tagged at the respective structure (paired analysis). The same test was used to compare densities of trout, bullhead, minnow and stone loach (of all age classes sampled) downstream of structures with upstream densities, combined for all connectivity-restored structures (paired analysis).

Obstacle permeability to bullhead and trout dispersal, pre- and post-restoration was analysed using Laplace kernel analyses (Pépino *et al*., 2012). Distances moved by brown trout and bullhead in 20 m connected longitudinal zones were natural-log transformed. Laplace double exponential kernel density functions were then used. The Laplace mixture kernel (f_{BLM}), which distinguishes between homogeneous and heterogeneous populations (Pépino *et al*. 2012), consists of two density functions of the barrier Laplace kernel (f_{BL}), one for sedentary individuals and one for mobile fish (Rodríguez 2010):

$$f_{BL}(x, \delta, k) = \begin{cases} f_L(x, \delta) + \exp\left(\frac{-|b|}{\delta}\right)(1 - k) f_L(x - b, \delta) & \text{for } x \geq b \text{ and } b < 0 \text{ as well as for } x \leq b \text{ and } b > 0 \\ \exp\left(\frac{-|b|}{\delta}\right) k f_L(x - b, \delta) & \text{for } x < b \text{ and } b < 0 \text{ as well as for } x > b \text{ and } b > 0 \end{cases}$$

$$f_{BLM}(x, s, \delta_s, \delta_m, k) = s\, f_{BL}(x, \delta_s, k) + (1 - s)\, f_{BL}(x, \delta_m, k)$$

For f_{BL}, x represents the distance from point of recapture to where the individual was first released (m), δ is the mean dispersal distance in the population (m), k is the permeability parameter on a scale from 0.0 (non-permeable) to 1.0 (fully permeable, no barrier effect) and b stands for the distance between the obstacle and the initial capture point. For f_{BLM}, s is the proportion of sedentary fish and δ_s and δ_m are mean dispersal distances of sedentary and mobile individuals (m), respectively. Numbers of tagged fish released initially per zone (capture) and fish dispersal distances (recaptures) were entered into separate $2n$ x $2n$ count matrices for each site (S1-S8), whereby recapture occasions (more than one per fish possible) during each recapture session in the 2013 and 2014 CMR campaigns were summed. Function f_{BLM} was then used to estimate parameters k and s for S1-S8 and associated fish populations. Packages HyperbolicDist, VGAM and bbmle were used to run the analyses in R version 3.2.3.

3. Results

3.1. Fish assemblages, densities and recolonization

Fish assemblages at surveyed structures (with the notable exception of upstream of S7 in all years and S8 in 2012, both in separate headwater streams) comprised mostly brown trout (61.3% of total) and, in lower densities, minnow (18.9% of total), bullhead (15.2% of total) and stone loach (4.5% of total) (***Table 3***). Eel and grayling were present in very low quantities (< 0.1% of fish caught) in all years. Benthic macro-invertebrate analyses showed moderate, good or high ecological quality status per site (***Table 3***), indicating that environmental conditions (particularly water quality) and invertebrate food availability for fishes were likely not limiting factors in the distribution and abundance of fishes during the study period. Habitat conditions for each site varied little between pre- and post-restoration (***Supp. Table 1*** and ***Supp. Table 2***, respectively).

Table 3: Density estimates per species (per 100 m^2) for 80 m longitudinal sections directly downstream (ds) and directly upstream (us) of each of the structures (S1-S8), ordered from the lower to the upper Deerness, using Carle & Strub's K-pass removal method, for summer 2013-2015 (and for S8 in autumn 2012 (*)). Shaded numbers represent structures pre-restoration, unshaded numbers post-restoration. bt: brown trout, bh: bullhead, m: minnow, sl: stone loach. NTAXA refers to the number of benthic macroinvertebrate families recorded; MINTA is a benthic macroinvertebrate derived biotic index of river habitat quality (Davy-Bowker *et al.* 2008). M: moderate, G: good, H: high (best), see text for further information.

Structure	bt			bh			m			sl			NTAXA			MINTA		
	2013	2014	2015	2013	2014	2015	2013	2014	2015	2013	2014	2015	2012	2013	2014	2012	2013	2014
S1 ds	38.1	38.6	32.5	6.5	6.7	9.2	8.2	7.2	8.6	1.7	2.8	0.0	-	-	-	-	-	-
S1 us	17.0	20.1	19.0	3.5	3.9	5.8	3.3	3.9	3.2	3.1	1.2	1.4	18	18	23	G	G	G
S2 ds	20.4	18.3	12.3	4.6	4.3	3.5	3.6	2.5	6.0	10.7	2.3	1.8	-	-	-	-	-	-
S2 us	17.8	21.8	25.9	3.8	4.8	4.4	2.8	3.7	11.9	2.4	1.7	2.4	16	18	20	G	G	M
S3 ds	15.2	17.5	10.5	3.2	4.1	5.4	8.3	6.0	6.0	2.9	1.3	1.0	-	-	-	-	-	-
S3 us	15.3	15.5	11.8	5.2	4.7	5.7	6.6	3.4	5.7	1.4	0.7	2.0	-	-	-	-	-	-
S4 ds	17.6	17.1	16.1	3.4	4.3	5.4	8.1	5.0	7.1	1.7	2.9	2.5	-	-	-	-	-	-
S4 us	21.7	23.0	21.5	4.6	5.2	3.7	12.2	4.1	7.0	1.5	1.9	0.0	-	20	20	-	G	G
S5 ds	22.4	20.6	12.1	4.3	6.9	6.1	5.1	8.5	6.1	2.7	2.0	2.0	-	-	-	-	-	-
S5 us	17.0	16.1	17.3	3.4	4.4	7.3	4.2	4.0	4.0	1.5	0.8	2.8	-	-	-	-	-	-
S6 ds	22.2	21.1	25.4	3.5	3.9	5.0	5.6	3.6	7.1	0.7	1.8	0.0	-	-	-	-	-	-
S6 us	10.9	11.7	19.6	1.6	2.1	5.8	0.8	2.5	1.7	1.2	0.8	0.0	-	18	17	-	M	M
S7 ds	22.2	24.5	15.0	11.6	15.0	6.0	16.7	9.5	7.0	3.2	1.0	3.0	-	-	-	-	-	-
S7 us	21.3	16.7	24.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	-	17	22	-	M	G
S8 ds	9.5* 31.3	34.8	30.8	25.7* 9.4	8.9	6.3	8.6* 16.5	17.0	9.4	0.0* 2.7	0.9	3.1	-	-	-	-	-	-
S8 us	7.3* 24.5	22.7	20.8	0.0* 5.7	7.9	4.6	0.0* 12.7	19.0	6.5	0.0* 2.4	1.4	0.0	19	18	21	H	M	G

Trout only were recorded upstream of S8 before its modification (finished, Oct 2012), while immediately downstream trout, bullhead and minnow were present. Following connectivity restoration at S8, bullhead, minnow and loach were recorded upstream and downstream of the structure, the latter at low densities only and not recorded upstream in 2015. Bullhead and minnow were recorded at increasing distances upstream, in summer 2013 (up to 120 m and 140 m above the structure for bullhead and minnow, respectively) and summer 2014 (up to 300 m and 280 m above the structure for bullhead and minnow, respectively). Additional support for the ascent of the pool-weir fishway and inferred recolonization by bullhead at S8 is evident from PIT and VIE tagging (***Table 4***). By contrast, no upstream passage of bullhead was recorded at S7 (***Table 4***), a control site of similar stream width and form where no mitigation measures were adopted. Although trout, bullhead, minnow and stone loach were found downstream of S7 over the period 2012-2015, only trout were recorded above the structure over the same period (***Table 3,*** surveyed discontinuously in suitable habitats up to ~700 m upstream in 2013 and 2014).

Comparing densities of trout, bullhead, minnow and stone loach (age classes combined) in the same reaches, between unrestored and connectivity-restored conditions (n = 5 structures restored by 2014), bullhead density upstream of the restored structures was significantly higher in 2014 than in 2013 (Wilcoxon signed rank test: Z = -2.201, P = 0.028) and loach density upstream of restored structures was marginally lower in 2014 than 2013 (Z = -1.992, P = 0.046); all other tests were non-significant. No significant differences in fish density were found at restored structures between 2014 and 2015 and between 2013 and 2015 for any species (n = 6 structures, Wilcoxon signed rank test, P > 0.05 in all cases). For control sites (n = 2), the sample size was too small for statistical comparison, but overall mean densities (all species of all captured age classes, for S3 and S7 combined) varied little downstream of the structures (2013-2014: -4.3%, 2014-2015: -9.2%, 2013-2015: -12.5%), and upstream (2013-2014: -9.7%, 2014-2015: +2.8%, 2013-2015: -7.3%). Analyses solely based on densities of age 0+ trout (length < 90 mm) showed an increase in density following restoration at four out of five restored structures (mean ± SD increase in 2015 relative to 2013: 15.5 ± 16.4%). Densities of age 0+ trout were higher downstream of two out of five sites (S5, S6) in 2015 compared to 2013 (mean ± SD: 26.5 ± 17.9%), and lower for the remaining three structures (27.7 ± 14.1%). The two control sites showed an increase in densities downstream (7.7 ± 3.8%) between the same years, while values were lower upstream of the structures by 8.9 ± 6.2%.

3.2. Capture-mark-recapture surveys of dispersal and passage

During the 2013 CMR campaign S1, S2 and S4-S6 were unrestored, but by spring 2014 all were, except S6 which was completed 10 days before the final recapture session in September 2014 (***Table 1***). The 2014 CMR campaign represents post-modification conditions for those sites except S6. Restoration at S8 was completed in autumn 2012; thus 2013 and 2014 CMR campaigns there reflect post-modification conditions, while at S3 and S7 they represent control pre-restoration conditions (***Table 1***). Totals of n = 864 brown trout and n = 153 bullhead were recaptured in 2013, and n = 394 trout and n = 77 bullhead in 2014 (***Supp. Table 3, Supp. Table 4)***. Single-pass catch efficiencies, calculated from depletion surveys at the sites, were 70.0% for trout and 69.0% for bullhead in 2013 and 67.8% and 65.7% respectively in 2014. Based on 20 m zonal CMR surveys, distance dispersed by trout (mean length 116.6 mm (50 - 338 mm)) and bullhead (mean length 72.8 mm (52 - 111 mm)) from the zone of capture met a leptokurtic distribution. Combining PIT tagged fish released at each structure, in each zone in 2013 (trout: n = 879; bullhead: n = 300) 53.5% of PIT tagged trout recaptures (204/382, mean length 116.4 mm) and 60.2% of PIT tagged bullhead recaptures (56/93, mean length 82.5 mm) stayed in the same 20 m stream section relative to their last known location. In 2014, 54.1% (226/418 recaptures, mean length 122.8 mm) and 63.4% (26/41 recaptures, mean length 82.9 mm) of all released PIT tagged trout (n = 815) and bullhead (n = 116) respectively did not move between stream sections. For VIE tagged individuals (total for 2013 and 2014: n = 2124 and n = 452 trout, respectively; n = 397 and n = 220 bullhead), a slightly greater proportion of bullhead recaptures (78/127 (61.4%) and 41/63 (65.1%)) than trout ones (422/734 (57.5%) and 98/159 (61.7%)) occurred in the same zone as previously for 2013 and 2014 respectively.

Using a barrier Laplace mixture model, where no discrimination is made between obstacle traverses in up- or downstream direction, barrier permeability (k) increased following connectivity restoration at all such structures (S1, S2, S4, S5; ***Fig. 2***, ***Table 4***). This was true for brown trout tagged with PIT (1+ and older age group, > 80 mm in length, mean factor of increase 2.36) and for those trout individuals VIE tagged (0+ age group, 50 - 79 mm in length, mean factor of increase 9.23). Structures where pre-/post-restoration CMR occurred during the study, were more permeable for bullhead in three out of four cases following restoration than before (S2, S4, S5, mean factor of increase 3.21, excluding S2 due to zero barrier traverses before connectivity restoration). Statistically significant increases post-intervention were particularly evident for Age 0+ trout and bullhead (***Table 4***). At control sites (S3, S7), barrier permeability was similar between years for all fish groups, except that permeability was significantly higher in 2014 for Age 0+ trout. (***Table 4***).

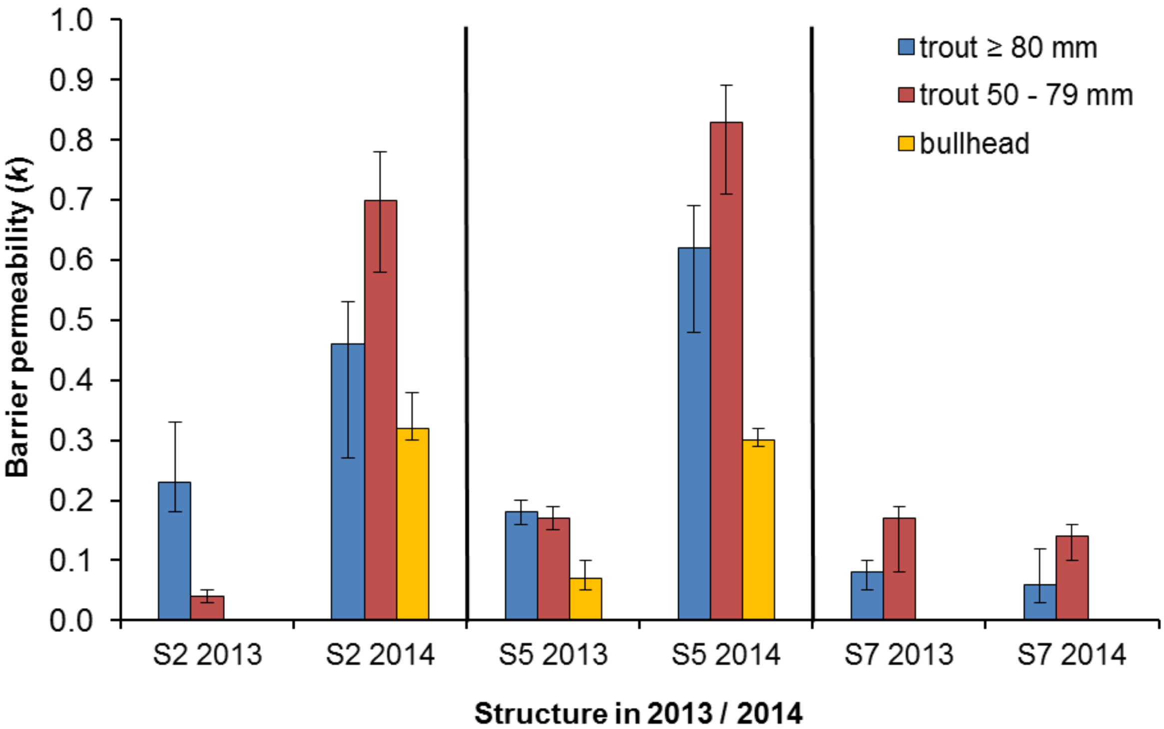

Figure 2: Examples of connectivity restoration effects on barrier permeability *k* (± 95% CI) for brown trout PIT tagged (trout ≥ 80 mm, blue), brown trout VIE tagged (trout 50 - 79 mm, red) and combined PIT and VIE bullhead (bullhead, orange), based on a Laplace kernel modelling approach of observed dispersal distance and barrier traverses. For illustration, structures at sites S2, S5 (both restored), and S7 (no restoration, control) are shown.

Table 4: Modelled barrier permeability parameters per structure, per species (brown trout of two size ranges, bullhead) for the 2013 and 2014 campaign, as estimated by the barrier Laplace mixture models approach (f_{BLM}). *k*: barrier permeability (scale from 0 - 1); *s*: proportion of sedentary individuals (scale from 0 - 1). 95% confidence intervals are shown in parentheses.

Species, body length	Site	Year	*k*	*s*
Trout ≥ 80 mm	S1	2013	0.15 (0.11-0.18)	0.62
		2014	0.41 (0.27-0.48)	0.66
	S2	2013	0.23 (0.18-0.33)	0.58
		2014	0.46 (0.27-0.53)	0.69
	S3	2013	0.00 (0)	0.47
		2014	0.13 (0.08-0.16)	0.59
	S4	2013	0.27 (0.21-0.38)	0.63
		2014	0.34 (0.31-0.36)	0.71
	S5	2013	0.18 (0.16-0.20)	0.56
		2014	0.62 (0.48-0.69)	0.48
	S6	2013	0.22 (0.18-0.24)	0.52
		2014	0.20 (0.18-0.23)	0.56
	S7	2013	0.08 (0.05-0.10)	0.62
		2014	0.06 (0.03-0.12)	0.57
	S8	2013	0.46 (0.42-0.51)	0.64
		2014	0.51 (0.46-0.53)	0.59
Trout 50-79 mm	S1	2013	0.06 (0.03-0.08)	0.70
		2014	0.46 (0.41-0.49)	0.51
	S2	2013	0.04 (0.03-0.05)	0.62
		2014	0.70 (0.58-0.78)	0.66
	S3	2013	0.08 (0.07-0.09)	0.67
		2014	0.35 (0.32-0.37)	0.56
	S4	2013	0.09 (0.07-0.10)	0.63
		2014	0.62 (0.57-0.66)	0.68
	S5	2013	0.17 (0.15-0.19)	0.62
		2014	0.83 (0.71-0.89)	0.67
	S6	2013	0.12 (0.07-0.14)	0.55
		2014	0.54 (0.49-0.61)	0.61
	S7	2013	0.17 (0.08-0.19)	0.51
		2014	0.14 (0.10-0.16)	0.57
	S8	2013	0.29 (0.27-0.30)	0.64
		2014	0.57 (0.50-0.68)	0.71
Bullhead	S1	2013	0.15 (0.10-0.21)	0.81
		2014	0.14 (0.13-0.16)	0.72
	S2	2013	0.00 (0)	0.68
		2014	0.32 (0.30-0.38)	0.74
	S3	2013	0.06 (0.05-0.08)	0.71
		2014	0.00 (0)	0.58
	S4	2013	0.18 (0.15-0.23)	0.66
		2014	0.39 (0.34-0.46)	0.72
	S5	2013	0.07 (0.05-0.10)	0.78
		2014	0.30 (0.29-0.32)	0.67
	S6	2013	0.21 (0.18-0.24)	0.62
		2014	0.23 (0.21-0.25)	0.69
	S7	2013	0.00 (0)	0.72
		2014	0.00 (0)	0.71
	S8	2013	0.18 (0.16-0.19)	0.61
		2014	0.25 (0.24-0.29)	0.64

CMR PIT tagged trout that passed upstream over each structure before connectivity restoration, were significantly larger relative to all tagged trout tagged at the structure (paired analysis), combined for all sites, for the 2013 CMR campaign (body length [mean ± SD]: 178.6 ± 17.6 mm vs 153.9 ± 38.2 mm; Wilcoxon signed rank test: $Z = -2.629$, $P = 0.009$). PIT tagged trout passing upstream at sites post-restoration were not significantly different in length than all tagged trout at liberty in the 2014 CMR campaign (body length [mean ± SD]: 135.4 ± 20.6 mm vs 148.3 ± 37.3 mm; Wilcoxon signed rank test: $Z = -1.742$, $P = 0.081$). No size-effect was found for PIT tagged trout that moved downstream past an obstacle pre-restoration compared to all tagged trout at liberty in 2013 (129.6 ± 15.5 mm vs 153.9 ± 38.2 mm, Wilcoxon signed rank test: $Z = -1.307$, $P = 0.191$). This was also true post-restoration (131.2 ± 16.3 mm vs 148.3 ± 37.3 mm, Wilcoxon signed rank test: $Z = -0.422$, $P = 0.673$). Sample sizes of PIT tagged bullhead dispersing past structures were too low for body length effect analysis.

3.3. Upstream passage efficiency of homing juvenile trout

Displacement CMR studies of trout in late summer 2012 demonstrated partial upstream permeability of obstacles for displaced trout (12-25 cm) at S1 (17 out of 50 (34.0%) displaced trout recaptured above the structure after ~3 weeks at liberty), S2 (3/28, 10.7%), S3 (6/33, 18.2%) and S8 (4/27, 14.8%), before restoration was undertaken. In August 2014, after restoration, at very low flows (~Q_{98}) 81.4% of experimentally displaced trout attempted to ascend the bypass channel at S2, during which time the weir was impassable as all stream flow was routed through the bypass, with a passage efficiency (of those attempting) of 70.1% (***Table 5***). For S8, (nature-like pool-weir and culvert combination) during very low flows (~Q_{98}) in September 2014, passage efficiency was 71.9%, while in November at slightly higher flow (~Q_{90}) it was 93.1% (***Table 5***). Time taken for trout to locate the fishway and duration of ascent differed between the three displacement studies (Kruskal-Wallis test, $K = 11.299$, $df = 2$, $P = 0.004$ and $K = 19.507$, $df = 2$, $P < 0.001$, respectively), being quicker for S2-Aug than S8-Sep and S8-Nov (Mann-Whitney test, $U = 481.0$, df = 1, $P < 0.001$ and $U = 133.0$, df = 1, $P < 0.001$, respectively). Trout displaced at both S8-Sep and S8-Nov were smaller than those at S2 (Mann-Whitney test, $U = 433.5$, df = 1, $P < 0.001$ and $U = 378.5$, df = 1, $P < 0.001$, ***Table 5***).

Table 5: Details of displaced trout attempting and succeeding in passing S2 and S8 respectively, following connectivity re-establishment works. If the interval time between successive detections at the fishway entrance was at least 30 s, it was counted as a separate attempt.

	S2 (Aug 2014)	S8 (Sep 2014)	S8 (Nov 2014)
Trout displaced	70	45	38
Mean length ± SD (range) [cm]	17.5 ± 2.4 (12.5-27.3)	14.5 ± 2.2 (12.0-21.9)	14.4 ± 1.9 (12.5-20.8)
Mean mass ± SD (range) [g]	64.5 ± 29.9 (18-200)	39.6 ± 23.5 (19-130)	34.3 ± 17.5 (21-104)
Proportion attempting passage	57/70 (81.4 %)	32/45 (71.1 %)	29/38 (76.3 %)
Passage efficiency	40/57 (70.1 %)	23/32 (71.9 %)	27/29 (93.1 %)
Mean time to locate fish pass ± SD (range) [m]	134.1 ± 121.4 (1.4-628.6)	606.9 ± 1115.3 (44.4-6178.2)	374.8 ± 446.1 (4.7-1659.8)
Mean ascent duration ± SD (range) [m]	53.0 ± 68.5 (8.7-269.3)	1668.7 ± 2684.7 (24.8-7648.6)	206.2 ± 292.0 (0.8-1048.2)
Mean no. attempts for successful trout (range)	1.5 (1-6)	5.8 (1-56)	6.3 (1-27)
Mean no. attempts for unsuccessful trout (range)	3.2 (1-11)	3.9 (1-7)	24.5 (7-42)

3.4. Radio telemetry of trout during the spawning migration

Post-remediation, twenty six adult sea trout and river-resident brown trout released and radio-tracked on the lower Browney (***Table 2***) initially remained below the gauging station (GS) during an extended period of dry weather, despite multiple visits to the proximity of the weir, and most eventually dropped downstream, including out of the tributary back into the main river (***Fig. 3***). Following a freshet, the majority of these trout were tracked upstream of GS (***Fig. 3***). Of the trout released on the lower Deerness (n = 13), 10 (77%) were located near to S1 within 24 h of release, showing motivation to migrate upstream. In total, 30 radio-tagged trout were found in the Deerness over the study period. When ordered from the lower Deerness (S1) to the upstream-most site on the Deerness where radio-tagged trout were still found (S6), the following numbers attempted and successfully passed the different barriers, whereby a fish located less than 100 m below a structure was regarded as attempting to pass it: S1: 23/30 (76.7%), 20/23 (86.9%); S2: 16/20 (80.0%), 13/16 (81.3%); S3: 12/13 (92.3%), 3/12 (25.0%); S4: 3/3 (100.0%), 3/3 (100.0%); S5: 3/3 (100.0%), 3/3 (100.0%); S6: 3/3 (100.0%), 3/3 (100.0%); S7: 0/3 (0.0%); S8: 0/3 (0.0%). Few trout (25.0%) ascended S3 over a variety of flow conditions (***Fig. 3***), even though spawning habitat is abundant upstream. Individuals that passed S3 continued their migration and were found up to 1.09 rkm upstream of S6 (***Fig. 3***). The cumulative passability, calculated as the product of individual passability values (Kemp and O'Hanley 2010), for the respective Deerness structures where attempts of passage were recorded (n = 6), was thus 0.177 ($0.869 \cdot 0.813 \cdot 0.250 \cdot 1.000 \cdot 1.000 \cdot 1.000$).

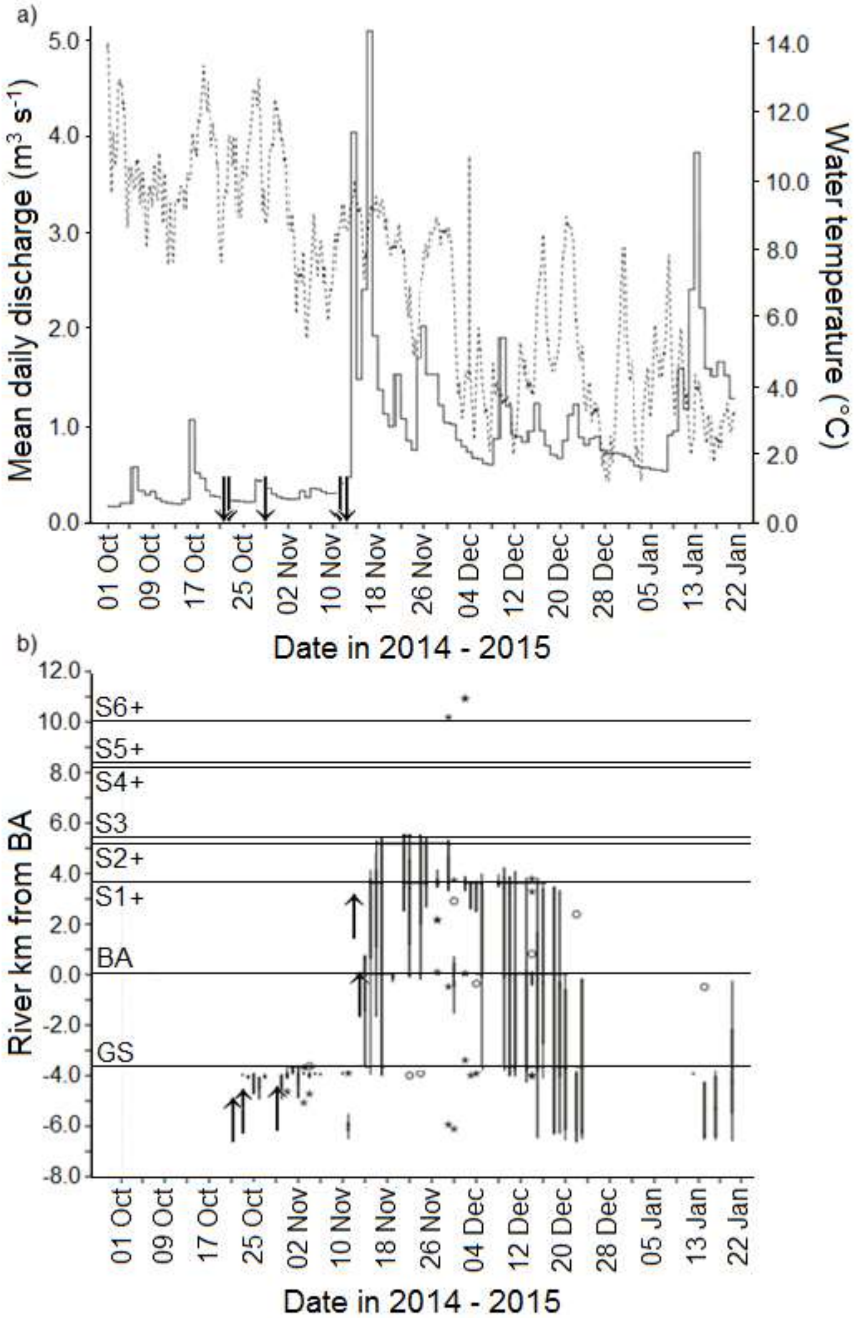

Figure 3: a) Mean daily discharge (m^3 s^{-1}, continuous line) at gauging station (GS) on the lower Browney and water temperature (°C, 15 min interval, dotted line) at S2 on the middle Deerness for the study period; b) distribution of radio-tagged adult sea trout / brown trout locations (median, 25% and 75% quartiles, circles and stars are outliers and extreme outliers, respectively) relative to bridge apron (BA), released over five sessions. Points of release (a: temporal; b: spatiotemporal) are indicated by bold arrow. Negative values indicate a downstream position relative to BA. Horizontal lines in b) indicate locations of in-stream structures (labelled adjacent to the y-axis, whereby restored structures during the tracking period are marked with a +); in order from the downstream-most structure on the lower Browney (GS) to the upstream-most location on the upper Deerness where radio-tagged trout were logged (S6). Only trout movement in the lower Browney (downstream of DBC) and in the Deerness is shown.

4. Discussion

This study demonstrates how multiple methods can be used *in situ* to quantify different aspects of the effectiveness of connectivity restoration in streams, for a range of species and life stages varying in size, dispersal tendency and swimming performance. In Europe, ecological quality indicators for fish, required under the Water Framework Directive (WFD), are measured by surveying fish assemblages and comparing these to reference conditions (Jepsen and Pont 2007). Thus, these are the data which European federal agencies record, against which to evaluate the effectiveness of habitat and connectivity restoration, and a similar situation often also occurs outside of Europe (McClelland *et al*. 2012). In this medium-term study, fish assemblage surveys mostly did not identify clear changes in fish populations due to connectivity restoration at multiple sites, but they did chart the rapid colonisation of a re-connected headwater, by comparison to a similar control site. Fish assemblage data gave information on diversity and distribution, and invertebrate data provided evidence of persisting good water quality and trophic diversity throughout the restoration period, identifying this not to be a limiting factor. Likewise, habitat in the study reaches remained stable over the study period. These fish assemblage data provide valuable contextual knowledge to connectivity restoration, but they do not provide mechanistic information on population connectivity and dispersal, making it difficult to determine the likely effectiveness of connectivity improvements on restoring fish diversity and ecological function in degraded stream systems. By contrast, telemetry methods were highly effective in quantifying rates of approach and passage and identifying migration bottlenecks, which is of importance for adaptive approaches in connectivity-restoration planning and implementation. A well-ordered experimental CMR design enabled dispersal and passage of small non-salmonids and juvenile salmonids (bullhead and brown trout, fish species with contrasting swimming and jumping capacities) to be quantified cost-effectively using the barrier permeability modelling approach. In combination, these methods provide much greater insight as to the effectiveness of connectivity restoration measures to achieve their objectives, across species and life stages with differing dispersal and recolonization potential.

In temperate regions of the northern hemisphere, much emphasis on physical reconnection of river and stream channels for fish passage at river infrastructure, and evaluating its effectiveness, has been given to salmonid requirements (Roscoe and Hinch 2010; Bunt *et al.* 2012). It has been suggested that a fish pass (or other connectivity restoration mitigation) should exceed 90 % overall passage efficiency in order to be fully functional (Lucas and Baras 2001) for fishes which are strongly migratory and rely on movement between distinct localities as part of their life history. Weaker swimmers, often small-bodied fishes, such as the more sedentary *Cottus* (Utzinger *et al.* 1998; Knaepkens *et al.* 2004), are often not accounted for in fish pass design and efficiency evaluations (Clay 1995, but see Weibel and Peter 2013), because they are regarded as non-migratory, yet they can be important contributors to the ecological quality and functionality of riverine communities. Although such species do not migrate between different habitats they, like all river animals, rely on dispersal potential between habitat patches for population persistence and recolonization (Albanese *et al.* 2009; Urban *et al.* 2009; Pépino *et al*. 2012; Radinger and Wolter 2014). Relatively little is known about the effect of longitudinal continuum restoration for river fishes, especially in degraded and rehabilitated habitats, despite its crucial importance for species distribution, species turnover and recolonization of newly available habitats (Detenbeck *et al.* 1992; Albanese *et al.* 2009) and for gene flow (Hanski 1998). Our study showed that greatly improved dispersal potential was obtained for weak as well as strong swimmers at most restored sites, including all sites where obstacles were physically removed, showing the ecological value of such removals even when the obstacles are small. However, the Laplace kernel analysis suggested that the steep rock-ramp at S1 remained a strong obstacle for bullhead, even though some dispersal was achieved before and after remediation. By contrast, while the rock ramp at S1 dramatically increased obstacle permeability for trout fry, parr and adults, multiple 0.54 m pipes with the unaltered (control) pipe bridge at S3 remained a major impediment for adult trout (25% passage efficiency), probably because of their narrow width constraining access and passage for larger fish, even during elevated water levels.

Restoration of diverse communities in modified streams and rivers relies on achieving effective connectivity for the wide range of native fishes rather than just a few select species (Lucas and Baras 2001; Langford *et al.* 2009; Gough *et al.* 2012). For fish communities, hydromorphological impacts are among the greatest problems to achieving good ecological functionality of streams and rivers, for example as expressed in the WFD (Kemp and O’Hanley 2010). Fish pass performance is often highly variable, with some passes working efficiently for one or a few species while working inadequately for other fishes (Bunt *et al.* 1999; Noonan *et al*. 2012). Facilitating effective recolonization to promote restoration of a stream fish assemblage towards reference conditions needs a paradigm shift towards meeting the dispersal capabilities of weaker-swimming species, rather than concentrating on the species with strong swimming performance. Washburn *et al.* (2015) propose a European fish pass monitoring standard; we contend that such a standard must include methods appropriate to measure the dispersal potential of weak-swimming fishes (such as the CMR approach and Laplace kernel analysis used here), to better test and support restoration measures that facilitate recolonization by such species. Targeting passage of larger species (including through possible implementation of European passage monitoring standards unsuited to small, uneconomically important species) risks poorer progress towards achieving EU WFD 'good ecological condition' for fish communities in streams and rivers that are currently degraded.

One of the objectives of ecological engineering restoration in streams is to achieve more natural species assemblages at densities closer to carrying capacity than in degraded conditions. Hence many evaluation studies measure assemblage structure in terms of species composition and density, by comparison to reference conditions, and change over time in response to intervention (e.g. Angermeier and Winston 1999; Gehrke *et al.* 2002; Gillette *et al.* 2005; Alexandre and Almeida 2010). This study showed that recolonization by small species (minnow and bullhead) could be rapid when access was provided to adjacent suitable habitat, showing the utility of simple assemblage surveys in documenting successful reconnection. These headwater populations were probably isolated, followed by a population decline and eventual extinction by industrial, agricultural or domestic pollution incidents (Knaepkens *et al.* 2006), yet when conditions subsequently improved, recolonization was limited by physical obstruction.

Alleviating river habitat fragmentation is not important only for adult fishes such as those migrating upriver to spawn (Forty *et al*. 2016). Young-of-the-year trout, competing for food and space, may disperse from areas of high fry density to lower density areas, a process possibly alleviated by effective passage solutions, so potentially reducing density dependent mortality (Armstrong *et al.* 2003). Fish dispersal is a result of the link between fitness and stream patch-specific characteristics; if fitness-decreasing variables are present in the area, emigration to other stream reaches is promoted (Gowan and Fausch 2002; Croft *et al.* 2003). Factors affecting dispersal are, for example, abundance of predators and amount of fish cover (Harvey *et al.* 1999; Gilliam and Fraser 2001), length of riffle habitat next to the reach (Schaefer 2001) and increased current velocity (Schaefer 2001). Changes in fish densities may not be a good indicator of restorative effects of alleviating fragmentation, as the area where fish originated from is often not clear or densities may be influenced by fluctuating environmental variables leading to varying recruitment success (Pretty *et al*. 2003). We found a small increase in age 0+ trout densities and bullhead, and a small decrease in loach densities, immediately upstream of restored structures compared to before intervention, probably due to increased suitability of local habitat for 0+ trout, rather than due to a wider increase in population. Although density or relative abundance estimates of fishes can be susceptible to error due to variations in fishing efficiency, often due to changes in environmental conditions (Jepsen and Pont 2007), catch efficiency remained high (65-70%) in our quantitative surveys. While many studies show that the distribution of fish species in modified stream and river systems is affected by connectivity disruption (Cote *et al.* 2009; Fullerton *et al.* 2010), this is not always the case. Branco *et al.* 2012 reported habitat variation may be more important, although interaction between these variables seems likely. Obstacles may be of differing passability and cause differing degrees of local habitat alteration. Low-head structures may become submerged when water levels rise, resulting in a partly permeable structure (Ovidio and Phillipart 2002).

In conclusion, this study demonstrates that habitat connectivity restoration at engineered in-stream structures on the Deerness has been effective for both strong swimmers (brown trout) and for those with limited swimming abilities (bullhead). When considering river reconnection schemes, we suggest that increasing emphasis needs to be placed upon ensuring whole fish community access (Gough *et al.* 2012; Cooke and Hinch 2013), unless there is a need to preclude invasive species (McLaughlin *et al*. 2013). Often, fish passage studies assess a modified facility only for stronger swimmers, yet it is crucial that a wide range of species with different swimming abilities is considered and that for rehabilitating degraded systems towards reference conditions, emphasis is shifted towards ensuring that dispersal of weaker swimmers, as well as passage of migrants, is achieved effectively.

Our study provides evidence that highly effective connectivity restoration within a tributary requires each and every obstacle to be addressed, since cumulative passage declines dramatically when even a single structure presents an obstacle. This study also shows the value of using an integrated combination of methods to gauge connectivity restoration for stream fish communities, certainly not relying upon fish density surveying alone.

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Appendix A. Supplementary data

Supplementary table 1: Habitat characteristics at each study site (*n* = 8), pre-restoration and separated between downstream (ds) and upstream (us) sections of the respective structure. Conducted at baseflow (*ca.* Q_{90}). Substrate - ho: high organic; si: silt; sa: sand; gr: gravel; pe: pebble; co: cobble; bo: boulder; be: bedrock. Flow - sm: still marginal; dp: deep pool; sp: shallow pool; dg: deep glide; sg: shallow glide; ru: run; ri: riffle. Fish cover type - dr: draped; uc: undercut; rt: roots; rk: rocks; ma: marginal.

		Water depth (%)				Substrate (%)								Instream vegetation (%)	Flow (%)							Canopy cover (%)	Fish cover (%)	Fish cover type	Bankside status (severe, moderate, light)			Overhanging boughs (%)
	Wet width (m)	0-20 cm	21-40 cm	41-80 cm	>80 cm	ho	si	sa	gr	pe	co	bo	be		sm	dp	sp	dg	sg	ru	ri				Collapse (%)	Erosion (%)	Trampling (%)	
S1 ds	4.3	60	15	15	10	0	5	5	15	25	25	15	10	20	10	15	10	10	25	10	20	40	35	dr, uc, rt, rk, ma	0;15;15	0;0;10	0;5;5	15
S1 us	5.1	10	5	15	70	0	10	30	15	5	15	15	10	10	5	45	10	30	10	0	0	50	30	uc, dr	0;5;15	0;5;5	0;0;0	20
S2 ds	4.7	60	15	10	15	5	10	10	5	30	30	5	5	20	10	15	15	15	20	15	10	35	35	uc, dr	0;5;10	0;5;5	0;5;5	20
S2 us	4.1	10	15	35	40	0	20	50	20	5	5	0	0	10	0	40	10	35	15	0	0	35	40	dr, uc, rt	0;10;10	0;0;10	0;5;10	15
S3 ds	4.2	35	30	30	5	0	10	15	10	20	25	10	10	15	5	20	15	10	15	30	5	45	35	dr, uc, rt, rk	0;0;10	0;5;10	0;0;10	10
S3 us	3.5	70	25	5	5	5	5	10	10	35	30	5	0	5	20	5	5	0	20	30	20	35	25	dr, uc, rt	0;5;10	0;0;0	0;5;10	10
S4 ds	3.8	50	20	20	10	0	10	15	10	20	30	10	5	10	5	20	20	5	20	20	10	40	15	uc, dr, rk	0;0;10	0;5;5	0;0;10	25
S4 us	3.7	25	50	20	5	0	10	40	5	20	20	5	0	5	15	10	25	10	25	10	5	45	15	dr, uc, rt	0;5;10	0;5;10	0;5;10	15
S5 ds	3.4	40	20	30	10	5	10	15	10	25	15	15	5	5	10	20	10	5	15	25	15	60	10	dr, uc, rt, rk, ma	0;5;10	0;0;10	0;0;0	5
S5 us	2.9	50	40	5	5	5	15	35	5	15	10	5	10	5	10	5	20	5	25	25	10	70	35	uc, dr	0;0;10	0;5;5	0;5;5	15
S6 ds	3.2	35	25	20	20	5	5	15	10	20	30	10	5	5	15	20	20	10	10	20	5	25	30	dr, uc, rt	0;0;15	0;5;5	0;5;10	20
S6 us	2.9	40	45	10	5	10	15	35	5	10	15	5	5	0	15	5	15	5	35	25	0	50	15	uc, dr, rk	0;5;10	0;5;10	0;5;10	15
S7 ds	2.7	30	40	15	15	0	10	15	10	25	25	10	5	10	15	20	10	5	15	20	15	70	20	dr, uc, rt, rk, ma	10;15;10	0;10;10	0;0;0	35
S7 us	2.0	30	45	15	10	5	15	20	10	20	25	5	0	15	15	10	5	5	20	30	15	40	25	uc, dr, rk	0;0;10	0;5;5	0;5;10	25
S8 ds	2.6	20	50	15	15	0	5	15	15	25	30	5	5	20	15	20	5	25	10	15	10	40	20	dr, uc, rt, rk, ma	10;15;10	10;20;25	0;5;10	45
S8 us	2.9	40	40	15	5	0	15	25	10	15	25	10	0	10	5	5	20	5	20	25	20	25	35	rk, uc, rt	0;0;10	0;0;5	0;0;5	15

Supplementary table 2: Habitat characteristics at each study site (n = 8), post-restoration and separated between downstream (ds) and upstream (us) sections of the respective structure. Conducted at baseflow (*ca.* Q_{90}). Substrate - ho: high organic; si: silt; sa: sand; gr: gravel; pe: pebble; co: cobble; bo: boulder; be: bedrock. Flow - sm: still marginal; dp: deep pool; sp: shallow pool; dg: deep glide; sg: shallow glide; ru: run; ri: riffle. Fish cover type - dr: draped; uc: undercut; rt: roots; rk: rocks; ma: marginal.

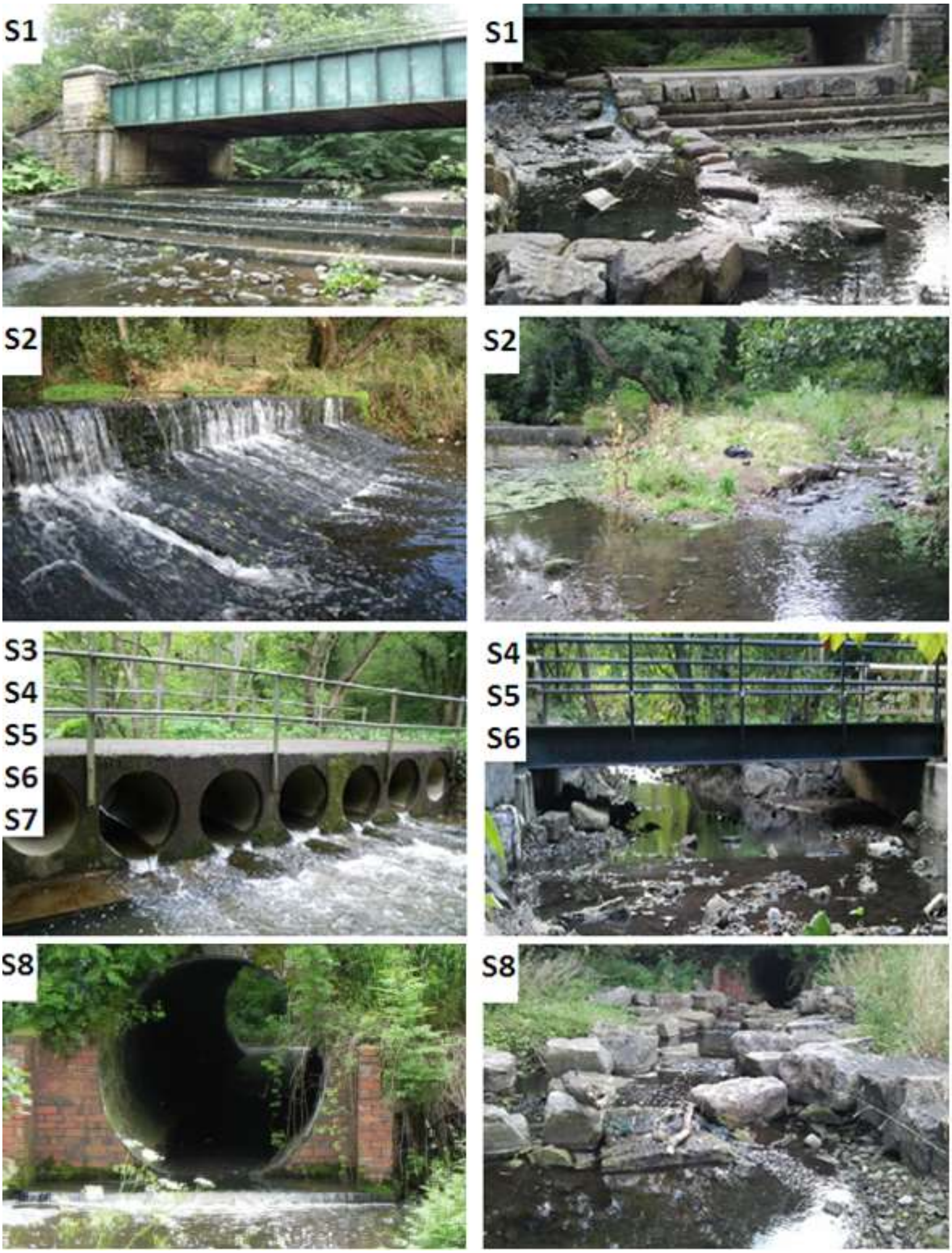
		Water depth (%)				Substrate (%)								Instream vegetation (%)	Flow (%)							Canopy cover (%)	Fish cover (%)	Fish cover type	Bankside status (severe, moderate, light)			Overhanging boughs (%)
	Wet width (m)	0-20 cm	21-40 cm	41-80 cm	>80 cm	ho	si	sa	gr	pe	co	bo	be		sm	dp	sp	dg	sg	ru	ri				Collapse (%)	Erosion (%)	Trampling (%)	
S1 ds	4.5	70	10	10	10	0	5	5	15	25	25	15	10	15	20	30	10	10	10	10	10	55	40	dr, uc, rt, rk, ma	0;15;20	0;0;10	0;0;0	25
S1 us	5.4	15	5	20	60	0	5	5	10	15	30	20	15	15	5	35	5	20	20	10	5	65	45	dr, uc, rt, rk, ma	0;5;10	0;0;10	0;0;0	30
S2 ds	5	50	20	15	15	5	10	10	5	30	30	5	5	10	10	10	5	10	15	30	20	20	25	dr, uc, rt	0;0;10	0;5;5	0;5;10	20
S2 us	4.2	10	15	50	25	0	10	35	20	10	10	10	5	5	5	30	10	30	15	5	5	45	30	dr, uc, rt, rk	0;0;10	0;5;5	0;5;10	25
S3 ds	4.5	25	40	25	10	0	5	15	15	25	30	5	5	10	5	10	10	20	20	25	10	30	25	dr, uc, rt	0;0;5	0;0;0	0;5;10	10
S3 us	3.7	65	20	10	5	5	10	15	10	30	25	5	0	5	15	5	5	5	20	25	25	25	25	dr, uc, rt	0;0;10	0;0;0	0;5;10	15
S4 ds	3.5	40	25	25	10	0	5	15	10	25	25	15	5	5	10	5	10	10	15	30	20	35	20	uc, dr, rk	0;0;15	0;5;5	0;5;10	20
S4 us	3.6	50	20	25	5	0	10	35	5	25	20	5	0	10	15	5	15	0	15	35	15	45	20	uc, rt	0;0;10	0;5;5	0;5;10	20
S5 ds	3.3	45	20	25	10	5	10	20	5	20	20	15	5	10	5	15	15	5	20	25	15	40	15	dr, uc, rt, rk	0;5;10	0;0;10	0;0;0	15
S5 us	3.1	80	15	5	0	5	10	15	5	25	25	10	5	5	20	0	5	0	20	40	15	55	20	uc, dr	0;0;15	0;5;5	0;5;10	15
S6 ds	3.5	40	20	20	20	10	10	20	10	10	15	20	5	15	15	15	15	10	10	25	10	15	20	dr, uc, rt	0;0;15	0;5;5	0;5;10	20
S6 us	3	70	20	10	0	0	5	25	5	25	35	5	0	5	25	5	10	0	20	35	5	70	15	dr, uc, rt, rk, ma	0;0;15	0;5;5	0;5;10	15
S7 ds	2.5	20	50	20	10	5	5	15	10	20	25	15	5	5	10	15	15	5	20	25	10	65	10	dr, uc, rt	0;5;10	0;0;10	0;0;0	15
S7 us	1.8	35	40	20	5	0	5	25	10	20	35	5	0	5	15	5	5	10	30	25	10	50	15	dr, uc, rt	0;0;15	0;5;5	0;5;10	25
S8 ds	2.8	15	45	30	10	5	0	10	15	25	30	10	5	25	10	20	10	20	15	20	5	25	35	uc, dr, rk	0;0;10	0;10;15	0;5;10	20
S8 us	2.7	60	20	10	10	0	5	15	10	25	35	10	0	5	5	10	15	5	15	20	30	40	20	uc, dr	0;0;5	0;0;5	0;0;5	15

Supplementary table 3: Numbers of PIT tagged brown trout (bt) and bullhead (bh) released per date and recaptured at least once (with recapture percentages in parentheses) per site (immediately downstream (ds) and upstream (us) of each structure). Data of the final survey in each CMR year is not listed, because no new fish were tagged in that survey.

		21 Aug 2013		**3 Sep 2013**		**3 Oct 2013**		**15 Jul 2014**		**30 Jul 2014**		**8 Sep 2014**	
		bt	**bh**	**bt**	**bh**	**bt**	**bh**	**bt**	**bh**	**bt**	**bh**	**bt**	**bh**
S1 ds	Released	55	8	62	8	31	7	77	10	42	2	12	0
	Recaptured	14 (25.4)	2 (25)	13 (20.9)	2 (25)	7 (22.5)	1 (14.2)	14 (18.1)	2 (20)	11	1 (50)	4 (33.3)	*n.a.*
S1 us	Released	66	0	54	1	36	24	66	1	52	11	67	0
	Recaptured	15 (22.7)	*n.a.*	13 (24)	0 (0)	4 (11.1)	4 (16.6)	16 (24.2)	0 (0)	14	2 (18.1)	12 (17.9)	*n.a.*
		19 Aug 2013		**1 Sep 2013**		**8 Oct 2013**		**19 Aug 2014**		**26 Aug 2014**		**1 Oct 2014**	
S2 ds	Released	27	0	47	11	49	14	15	1	9	0	0	9
	Recaptured	7 (25.9)	*n.a.*	12 (25.5)	2 (18.1)	11 (22.4)	3 (21.4)	5 (33.3)	0 (0)	3 (33.3)	*n.a.*	*n.a.*	2 (22.2)
S2 us	Released	18	0	14	5	3	2	21	2	32	1	0	5
	Recaptured	4 (22.2)	*n.a.*	3 (21.4)	1 (20)	0 (0)	0 (0)	6 (28.5)	1 (50)	9 (28.1)	0 (0)	*n.a.*	1 (20)
		19 Aug 2013		**2 Sep 2013**		**9 Oct 2013**		**19 Aug 2014**		**27 Aug 2014**		**2 Oct 2014**	
S3 ds	Released	20	0	11	5	1	3	23	0	23	1	0	4
	Recaptured	6 (30)	*n.a.*	3 (27.2)	1 (20)	0 (0)	1 (33.3)	5 (21.7)	*n.a.*	7 (30.4)	0 (0)	*n.a.*	1 (25)
S3 us	Released	7	0	26	19	22	15	16	0	20	3	0	7
	Recaptured	2 (28.5)	*n.a.*	5 (19.2)	4 (21)	5 (22.7)	2 (13.3)	5 (31.2)	*n.a.*	4 (20)	1 (33.3)	*n.a.*	1 (14.2)
		13 Aug 2013		**19 Sep 2013**		**13 Oct 2013**		**9 Jul 2014**		**28 Jul 2014**		**18 Aug 2014**	
S4 ds	Released	23	12	22	2	0	0	31	13	10	2	0	0
	Recaptured	6 (26)	2 (16.6)	5 (22.7)	1 (50)	*n.a.*	*n.a.*	9 (29)	2 (15.3)	3 (30)	0 (0)	*n.a.*	*n.a.*
S4 us	Released	17	6	10	4	0	0	34	9	4	4	0	0
	Recaptured	3 (17.6)	1 (16.6)	3 (30)	1 (25)	*n.a.*	*n.a.*	10 (29.4)	2 (22.2)	1 (25)	1 (25)	*n.a.*	*n.a.*
		14 Aug 2013		**20 Sep 2013**		**14 Oct 2013**		**9 Jul 2014**		**27 Jul 2014**		**17 Aug 2014**	
S5 ds	Released	19	8	9	4	0	0	46	8	5	4	0	0
	Recaptured	7 (36.8)	2 (25)	2 (22.2)	1 (25)	*n.a.*	*n.a.*	13 (28.2)	2 (25)	1 (20)	1 (25)	*n.a.*	*n.a.*
S5 us	Released	33	16	23	10	0	0	15	5	18	0	0	0
	Recaptured	9 (27.2)	3 (18.7)	7 (30.4)	2 (20)	*n.a.*	*n.a.*	4 (26.6)	1 (20)	4 (22.2)	*n.a.*	*n.a.*	*n.a.*
		12 Aug 2013		**16 Sep 2013**		**12 Oct 2013**		**18 Jul 2014**		**4 Aug 2014**		**30 Sep 2014**	
S6 ds	Released	30	18	33	5	0	0	43	1	41	5	14	0
	Recaptured	7 (23.3)	3 (16.6)	8 (24.2)	1 (20)	*n.a.*	*n.a.*	11 (25.5)	0 (0)	11	1 (20)	4 (28.5)	*n.a.*
S6 us	Released	12	4	41	9	0	0	7	0	13	3	35	1
	Recaptured	4 (33.3)	1 (25)	11 (26.8)	2 (22.2)	*n.a.*	*n.a.*	2 (28.5)	*n.a.*	4 (30.7)	1 (33.3)	8 (22.8)	0 (0)
		15 Aug 2013		**15 Sep 2013**		**15 Oct 2013**		**17 Jul 2014**		**5 Aug 2014**		**12 Sep 2014**	
S7 ds	Released	29	21	32	4	0	0	26	10	30	0	0	0
	Recaptured	9 (31)	4 (19)	9 (28.1)	0 (0)	*n.a.*	*n.a.*	6 (23)	2 (20)	8 (26.6)	*n.a.*	*n.a.*	*n.a.*
S7 us	Released	21	0	44	0	0	0	14	0	19	0	26	0
	Recaptured	6 (28.5)	*n.a.*	13 (29.5)	*n.a.*	*n.a.*	*n.a.*	4 (28.5)	*n.a.*	5 (26.3)	*n.a.*	7 (26.9)	*n.a.*
		7 Jul 2013		**14 Aug 2013**		**29 Aug 2013**		**16 Jul 2014**		**29 Jul 2014**		**1 Sep 2014**	
S8 ds	Released	26	47	35	31	40	23	34	10	40	1	24	0
	Recaptured	7 (26.9)	6 (12.7)	6 (17.1)	4 (12.9)	8 (20)	3 (13)	10 (29.4)	2 (20)	10 (25)	0 (0)	5 (20.8)	*n.a.*
S8 us	Released	42	8	28	6	34	2	18	6	23	3	48	4
	Recaptured	11 (26.1)	1 (12.5)	3 (10.7)	1 (16.6)	5 (14.7)	0 (0)	5 (27.7)	1 (16.6)	7 (30.4)	1 (33.3)	11 (22.9)	1 (25)

Supplementary table 4: Numbers of VIE tagged brown trout (bt) and bullhead (bh) released per date and recaptured at least once (with recapture percentages in parentheses) per site (immediately downstream (ds) and upstream (us) of each structure). Data of the final survey in each CMR year is not listed, because no new fish were tagged in that survey.

		21 Aug 2013		**3 Sep 2013**		**3 Oct 2013**		**15 Jul 2014**		**30 Jul 2014**		**8 Sep 2014**	
		bt	**bh**	**bt**	**bh**	**bt**	**bh**	**bt**	**bh**	**bt**	**bh**	**bt**	**bh**
S1 ds	Released	76	24	163	20	157	29	26	9	29	5	24	9
	Recaptured	20 (26.3)	5 (20.8)	28 (17.1)	3 (15)	31 (19.7)	5 (17.2)	5 (19.2)	2 (22.2)	6 (20.6)	1 (20)	5 (20.8)	2 (22.2)
S1 us	Released	67	8	161	19	156	24	11	5	11	4	16	7
	Recaptured	18 (26.8)	2 (25)	21 (13)	3 (15.7)	35 (22.4)	4 (16.6)	2 (18.1)	1 (20)	2 (18.1)	0 (0)	4 (25)	1 (14.2)
		19 Aug 2013		**1 Sep 2013**		**8 Oct 2013**		**19 Aug 2014**		**26 Aug 2014**		**1 Oct 2014**	
S2 ds	Released	101	11	153	7	142	15	13	2	13	4	15	9
	Recaptured	31 (30.6)	2 (18.1)	29 (18.9)	1 (14.2)	28 (19.7)	3 (20)	3 (23)	0 (0)	3 (23)	1 (25)	3 (20)	2 (22.2)
S2 us	Released	6	6	7	4	6	4	7	0	5	1	5	3
	Recaptured	1 (16.6)	1 (16.6)	2 (28.5)	1 (25)	1 (16.6)	1 (25)	2 (28.5)	*n.a.*	1 (20)	0 (0)	1 (20)	1 (33.3)
		19 Aug 2013		**2 Sep 2013**		**9 Oct 2013**		**19 Aug 2014**		**27 Aug 2014**		**2 Oct 2014**	
S3 ds	Released	0	0	1	3	0	3	6	6	3	1	2	1
	Recaptured	*n.a.*	*n.a.*	0 (0)	1 (33.3)	*n.a.*	0 (0)	1 (16.6)	1 (16.6)	0 (0)	0 (0)	0 (0)	0 (0)
S3 us	Released	9	8	32	11	51	13	4	2	7	3	15	4
	Recaptured	2 (22.2)	1 (12.5)	7 (21.8)	2 (18.1)	11 (21.5)	3 (23)	1 (25)	0 (0)	2 (28.5)	0 (0)	3 (20)	1 (25)
		13 Aug 2013		**19 Sep 2013**		**13 Oct 2013**		**9 Jul 2014**		**28 Jul 2014**		**18 Aug 2014**	
S4 ds	Released	84	15	94	19	0	0	18	6	10	3	10	7
	Recaptured	24 (28.5)	3 (20)	22 (23.4)	3 (15.7)	*n.a.*	*n.a.*	4 (22.2)	1 (16.6)	2 (20)	0 (0)	2 (20)	2 (28.5)
S4 us	Released	60	6	19	5	0	0	8	4	4	1	6	4
	Recaptured	19 (31.6)	1 (16.6)	4 (21)	1 (20)	*n.a.*	*n.a.*	2 (25)	1 (25)	1 (25)	0 (0)	1 (16.6)	1 (25)
		14 Aug 2013		**20 Sep 2013**		**14 Oct 2013**		**9 Jul 2014**		**27 Jul 2014**		**17 Aug 2014**	
S5 ds	Released	27	10	12	1	0	0	9	3	7	4	9	3
	Recaptured	8 (29.6)	2 (20)	3 (25)	0 (0)	*n.a.*	*n.a.*	2 (22.2)	0 (0)	1 (14.2)	1 (25)	2 (22.2)	1 (33.3)
S5 us	Released	74	21	89	23	0	0	8	5	6	5	15	6
	Recaptured	17 (22.9)	5 (23.8)	21 (23.5)	4 (17.3)	*n.a.*	*n.a.*	2 (25)	1 (20)	1 (16.6)	1 (20)	3 (20)	1 (16.6)
		12 Aug 2013		**16 Sep 2013**		**12 Oct 2013**		**18 Jul 2014**		**4 Aug 2014**		**30 Sep 2014**	
S6 ds	Released	147	21	96	22	0	0	13	10	12	11	15	13
	Recaptured	35 (23.8)	4 (19)	23 (23.9)	4 (18.1)	*n.a.*	*n.a.*	3 (23)	2 (20)	2 (16.6)	2 (18.1)	3 (20)	2 (15.3)
S6 us	Released	67	15	64	28	0	0	8	9	9	5	18	12
	Recaptured	16 (23.8)	3 (20)	15 (23.4)	5 (17.8)	*n.a.*	*n.a.*	2 (25)	1 (11.1)	2 (22.2)	1 (20)	4 (22.2)	2 (16.6)
		15 Aug 2013		**15 Sep 2013**		**15 Oct 2013**		**17 Jul 2014**		**5 Aug 2014**		**12 Sep 2014**	
S7 ds	Released	35	11	61	31	0	0	12	13	17	15	15	13
	Recaptured	9 (25.7)	3 (27.2)	12 (19.6)	6 (19.3)	*n.a.*	*n.a.*	2 (16.6)	2 (15.3)	3 (17.6)	3 (20)	3 (20)	2 (15.3)
S7 us	Released	32	0	50	0	0	0	11	0	11	0	12	0
	Recaptured	8 (25)	*n.a.*	9 (18)	*n.a.*	*n.a.*	*n.a.*	2 (18.1)	*n.a.*	2 (18.1)	*n.a.*	2 (16.6)	*n.a.*
		7 Jul 2013		**14 Aug 2013**		**29 Aug 2013**		**16 Jul 2014**		**29 Jul 2014**		**1 Sep 2014**	
S8 ds	Released	50	0	37	13	21	14	23	7	18	9	12	7
	Recaptured	7 (14)	*n.a.*	7 (18.9)	2 (15.3)	4 (19)	3 (21.4)	5 (21.7)	1 (14.2)	4 (22.2)	2 (22.2)	2 (16.6)	1 (14.2)
S8 us	Released	131	6	98	6	79	12	20	4	13	7	7	6
	Recaptured	28 (21.3)	1 (16.6)	19 (19.3)	1 (16.6)	16 (20.2)	2 (16.6)	4 (20)	1 (25)	3 (23)	1 (14.2)	1 (14.2)	1 (16.6)



Supplementary figure 1: Selection of photographs of structures studied on the River Deerness, grouped per type of structure for S1-S8 (see ***Table 1***, ***Fig. 1***), before (left) and after (right) restoration actions were completed, where applicable. All pictures were taken under baseflow conditions, except for S8 pre-mitigation. S1, stepped weir and with part-width rock ramp pass; S2, sloping plus step weir and with nature-like bypass; S3-S7, pipe bridge fords with full channel width single span bridges for S4-S6; S8, pipe culvert with nature-like pool-weir approach raising tailwater level.

Supplementary figure 2: Example of a VIE -marked bullhead, showing clear pink and green marks on the anatomical left and right side of the anal fin. This fish was thus captured, tagged, recaptured, tagged, recaptured.

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